JOURNAL OF FIELD ORNITHOLOGY
Formerly BIRD-BANDING
A Journal of Ornithological Investigation

VOL. 54, NO. 2 SPRING 1983 PAGES 113–224

J. Field Ornithol., 54(2):113–122

TIMING OF BREEDING AND MIGRATIONS IN A POPULATION OF LEAST FLYCATCHERS IN MANITOBA

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Hussell's (1980) analysis of fall specimens of the Least Flycatcher (*Empidonax minimus*) from North and Central America showed clearly that adults started migrating in early July and began to arrive on the wintering grounds in August, whereas the immatures migrated a month or so later. These results were consistent with the patterns of fall migration in this species determined in southern Ontario (Hussell et al. 1967, Hussell 1981) and Kansas (Ely 1970).

Hussell (1980) indicated that detailed observations of the disappearance of adult Least Flycatchers from the nesting grounds in relation to the independence of the young are needed to clarify the information obtained in these studies. We obtained such information in 1981 from a population that nests in high numbers on the forested dune ridge that separates Lake Manitoba and the Delta Marsh, Manitoba. Almost daily mistnetting from early May through August and intermittently in September and early October permitted us to determine the timing of migrations at this northern locality in the Least Flycatcher's breeding range. Adults banded during the breeding season and young banded as nestlings and others later as free-flying juveniles provided individuals of known status for potential recapture later in the season on our study area. The information derived from banding is discussed against a background of known clutch initiation and realized or projected dates of fledging in this population.

STUDY AREA AND METHODS

For the past 10 years Sealy and co-workers have studied the ecology of passerines that nest densely along the forested dune ridge that separates Lake Manitoba and the Delta Marsh, Manitoba. The 3-km portion of this ridge that is our study area (see map in Sealy 1980, MacKenzie 1982) is located on the properties of the University of Manitoba Field Station (Delta Marsh), about 5 km west of Delta, Manitoba, and the adjacent Portage Country Club.

Most of the projects have involved banding and marking birds, and in 1980, 61 adult Least Flycatchers were banded between 15 May and 25 June, most of which were probably resident breeders. In 1981, 416 Least Flycatchers were banded between 17 May and 23 September and

represent spring and "fall" migrants, breeders, and young reared on and probably also off the study area. All of these birds were caught in mist nets that were operated almost daily 14 May–8 July 1980 and 10 May–3 September 1981. Nets were operated intermittently from 6 September to 6 October 1981 (see footnote 5, Table 1). Seventy-three nests were studied in 1981 and 76 nestlings were banded at about 9 days of age in 25 of these nests. The total number of individuals banded in 1981 therefore was 492.

We aged Least Flycatchers according to the criteria outlined by Hussell (1980); that is, on the basis of color and wear of the greater wing coverts, remiges, and rectrices. We confirmed the reliability of this aging method when individuals banded as adults during the breeding season or as nestlings were recaptured and examined later during the post-breeding period. We define a "known resident" adult as one captured during two or more periods of the summer. Adults are assumed to be present on the study area between captures. Thus, a bird banded initially on 23 May and recaptured on 2 July is a "known resident" that was not recaptured between 26 May and 29 June. Between 30 June and 3 July, the bird is considered simply as a recapture and if not captured later is no longer a "known resident."

Each bird's flattened wing was measured to the nearest .5 mm. Numbered aluminum bands were placed on each individual. Individuals were examined for wing, tail, and body molt. Body molt was recorded as present (+) or absent (−). This method provides incomplete information on the extent of body molt, and nothing on its stage. It does reveal, however, the timing of the initiation of the first prebasic molt (of HY individuals) and later prebasic molts (in AHY individuals).

The following voucher specimens of Least Flycatchers taken on the study area have been deposited in the University of Manitoba Zoology Museum (UMZM): UMZM 705, HY ♀, 18 July 1976; UMZM 1851, HY ♂, 9 August 1981 (banded as a nestling on 23 June 1981); UMZM 706, AHY ♂, 29 May 1973; UMZM 704, AHY ♀, 10 June 1973, UMZM 707, AHY ♀, 19 May 1981.

Dates of Least Flycatcher clutch initiation were obtained by direct observations of nests during the egg-laying stage and by calculating the initiation date of those clutches that were found after they were completed, but whose hatching dates were known. Post-dating was accomplished by observing that Least Flycatchers generally lay one egg per day (Sealy, pers. obs.) and have an incubation period of about 13 days (Walkinshaw 1966). Fledging dates were obtained by direct observation of successful nests. In addition, the approximate dates nestlings would have fledged, in nests that failed, were calculated for nests where the clutch initiation or hatching dates were known by adding the incubation period and/or the known nestling period (=15 days, Walkinshaw 1966) to the egg-laying period.

TABLE 1. Numbers of adult and immature Least Flycatchers captured and recaptured on the dune-ridge forest, Delta Marsh, Manitoba, in 1981.

5-day periods		Total captured	AHY[1,2]	HY[1,3]	Known residents not recaptured	
					AHY	HY
May	11–15	4	4			
	16–20	12	12			
	21–25	13	11 (2)		1	
	26–30	23	21 (2)		3	
June	31–4	23	20 (3)		9	
	5–9	10	10		12	
	10–14	11	7 (4)		14	
	15–19	6	4 (2)		14	
	20–24	13	9 (4)	9[4]	14	
	25–29	23	18 (5)	21[4]	7	3
July	30–3	13	11 (2)	37[4]	6	13
	4–8	9	4 (5)	3[4]	4	19
	9–13	15	13 (2)		3	20
	14–18	32	27 (1)	3 (1)	1	19
	19–23	28	14 (1)	10 (3)[4]		17
	24–28	23	8 (1)	8 (6)		13
	29–2	36	4	29 (3)		9
Aug	3–7	47	3	40 (4)		9
	8–12	52	6	37 (9)		2
	13–17	39		36 (3)		
	18–22	22		22		
	23–27	12		12		
	28–1	5	1	4		
Sept[5]	2–6	6		6		
	7–11					
	12–16	1		1		
	17–21	2		2		
	22–26	2		2		
Oct[5]	27–1					
	2–6					

[1] We recognized two age classes of free-flying birds: Hatching Year (HY) birds were hatched in the current calendar year; and After-Hatching-Year (AHY), or birds that are older. Local (L) birds were banded as nestlings or as flightless fledglings, and many were recaptured in nets later on the study area.

[2] Numbers in parentheses are recaptures of individuals banded in 1980, which returned to the study area in 1981, and of those banded in 1981. The last individual was recaptured on 27 July.

[3] Numbers in parentheses are recaptures of individuals banded as nestlings and as HY birds in 1981. The last recapture was on 17 August.

[4] June 20 to July 8 young were all local birds. Three of the young banded between July 19 and 23 were local young.

[5] Netting occurred on September 1–3, 6, 12–13, 16–17, 22–23, 28, and October 5–6.

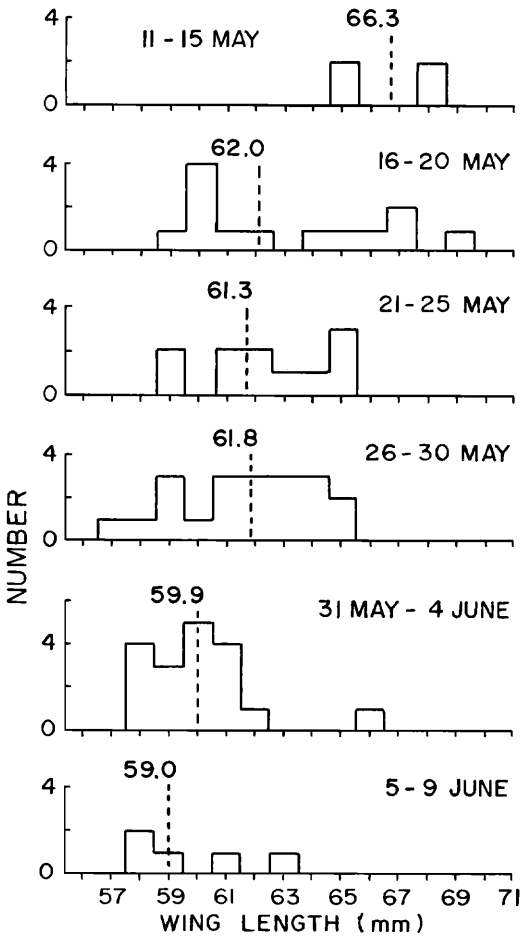

FIGURE 1. Distribution of flattened wing lengths of banded birds in relation to date during spring migration on the dune-ridge forest, Delta Marsh, Manitoba, 1981. Vertical broken lines indicate median wing lengths.

RESULTS

Table 1 shows the total and the numbers of adult (AHY) and juvenile (HY) Least Flycatchers netted in 5-day periods during the migration and breeding periods. The first Least Flycatcher in spring, 1981, was a single individual observed on 7 May on the study area by H. E. den Haan (pers. comm.). None was netted during the first day of netting (10 May), but on 11 May many were present and 3 were netted. The first recaptures in 1981, on 25 May, were of 2 individuals banded on the study area in 1980. Individuals banded as early as 19 May were recaptured later on the study area (Table 1), indicating that resident birds were on the study area by at least that date. It is likely that indi-

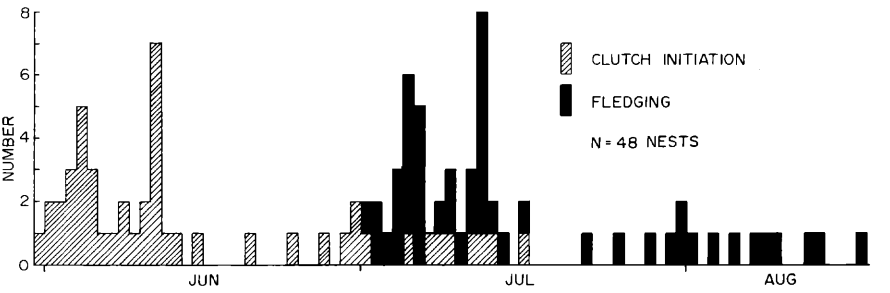

FIGURE 2. Dates of clutch initiation and realized or potential fledging dates of the Least Flycatcher on the dune-ridge forest, Delta Marsh, Manitoba, 1981.

viduals migrating to points beyond our study area arrive first in spring but do not stay, and hence are not recaptured (Table 1). Our sample of Least Flycatchers returning in spring reveals also that the longer-winged males return before the females, as is suggested by the wing length data in Fig. 1 (see also Ely 1970, Hussell 1981) [F test: $F(5,69) = 8.17$, $P < .005$]. Hussell's larger sample of wing lengths of spring migrants suggests that older males may return before one-year-old males and that the same order of return of the females prevails.

Clutch initiation in 1981 spanned 31 May through 16 July and fledging was from 1 July through 7 August in those nests under observation (Fig. 2), although most of the later nests failed (Table 2), and their "fledging" dates were therefore calculated. It is likely that at least one brood fledged on our study area after 16 August (Fig. 2). Four incompletely developed young, capable of flight, were netted together on 6 September. Sealy found a Least Flycatcher nest on 8 August 1979 that contained 4 "half-grown" nestlings. These young probably would have fledged in mid-August or slightly later that year. Nice and Collias (1961)

TABLE 2. Success of Least Flycatcher clutches on the dune-ridge forest, Delta Marsh, Manitoba, in relation to date of their initiation, 1981.[1]

Period	Number of nests[2]	Number of successful nests	Success (%)
31 May–9 June	31	19	61.3
10–19 June	20	12	60.0
20–29 June	5	1	20.0
30 June–9 July	5	1	20.0
10–20 July	4	1	25.0

[1] A successful nest is one in which at least one Least Flycatcher fledged.

[2] The number of nests whose clutch initiation dates are known to within 10 days is greater than that known to the nearest day (see Fig. 1).

reported a late fledging date (27 July) for a nest that they observed 5 km east of our study area on the dune ridge.

Observations in 1981 revealed that newly fledged young are tended by both parents. We did not determine, however, whether both parents tended young up to their independence. The period of post-fledging parental care is 2 weeks or slightly more. The first HY individual netted, on 17 July 1981, had been banded as a nestling on 23 June and had fledged on 3 July from its nest, about 30 m from the net site. This individual showed essentially complete development of its remiges and rectrices and was capable of flight. We cannot be sure, however, that it was indeed independent of its parent(s) although within a few days large numbers of HY individuals were being netted (Table 1). Davis (1959) observed in Virginia that both the male and female care for the young for up to 20 days post-fledging. This suggests that the earliest fledged young on our study area were independent by mid-July. The almost incessant vocalizing by Least Flycatchers ceased abruptly in late July (as noted also by Nice and Collias 1961) possibly because the young in most broods were now independent and/or these adults had left the dune ridge (Table 1). Adults observed still tending nests in early to mid-August called frequently.

Most nests whose clutches were initiated after late June failed (Table 2). These nests probably represent renesting attempts, where clutches that failed earlier were replaced. Renesting by Least Flycatchers has been reported elsewhere (Davis 1959, Walkinshaw 1966) but second broods apparently are rare (Walkinshaw 1966). We have no evidence of second broods being attempted on our study area, although Bent (1942: 216) stated (without presenting evidence) that two broods are "often, if not regularly" raised in the southern portion of its range (see also Hoffman 1901). Assuming that the period of post-fledging parental care does not vary geographically, adults that are tending young which have fledged as late as 17 August on our study area (Fig. 2) would be tied to the study area until at least early September.

Molt of the remiges and rectrices did not occur in AHY Least Flycatchers on the breeding ground, agreeing with Dwight's (1900), Johnson's (1963), and Hussell's (1980, 1981) findings that wing and tail molt of adults occurs after migration on the wintering grounds. Body molt, however, occurred in both age classes on the breeding ground, or while individuals were dispersing or migrating (Table 3).

DISCUSSION

Our findings for the fall exodus and movement of the Least Flycatcher from and through a breeding area in southern Manitoba point convincingly to a strongly asynchronous departure (and passage) of age groups, with most of the adults leaving the study area by mid-July, a few weeks before the last juveniles (Table 1). These observations confirm the existence of differential scheduling of the fall migration by old and young Least Flycatchers that has been described by Hussell et al. (1967), Ely (1970), and Hussell (1980, 1981) for several geographic regions.

TABLE 3. Body molt of Least Flycatchers, 1981.

Bi-weekly periods[1]	Number of AHY		Number of HY	
	(−)	(+)	(−)	(+)
1–15 July	32	14		
16–31 July	2	39		30
1–15 August	2	8	1	98
16–31 August			8	37
1–15 September		1	1	9
16–30 September				4

[1] Recaptures are not included.

Clench (1969) reported no age-related differences in the timing of fall migration in southwestern Pennsylvania from 1964 to 1967, but recent information from there analyzed by Hussell (1981) shows a pattern similar to that described above.

No adults banded on our study area before 1 July were recaptured after 27 July (Table 1), and only a few adults, all unbanded, were netted up to 11 August, with one captured on 1 September (Table 1). The few recaptures after 18 July of adults banded during the period of major breeding intensity by this population (Fig. 2) suggest strongly that these adults left the study area by mid-July. Such adults had perhaps raised young successfully, were non-breeders, or were possibly failed breeders. It appears also that by mid-July, adults from outside the study area were passing through as the number of unbanded individuals increased dramatically between 14 and 18 July (Table 1) before decreasing until only one was captured after 11 August. The adults' diminished territorial ties, as the young begin to gain independence in mid-July, may promote greater movement of breeders on the study area resulting in an increase in captures in late July. However, we might then expect that a greater proportion of the individuals netted at this time would be recaptures of birds banded previously. This was not the case (see Table 1). Recapture data are somewhat deceiving, however, because not all individuals on the study area are recaptured. Young in broods that fledged as late as 16 August would be tended by adults perhaps up to the end of August, if indeed the period of post-fledging parental care is as long as it is earlier in the season. One adult whose young fledged on the study area in mid-August had been banded earlier, but attempts to recapture it failed. Also, the recapture rate of adults (from 21 May through 18 July 1981 when recaptures were obtained) was only 20.6%.

No HY individuals known or suspected to have been reared on the study area in 1981 were recaptured after 17 August (Table 1). This abrupt cessation of recaptures of immatures probably indicates that these individuals had left their rearing area by this time and possibly were being replaced now by migrating individuals, or by young that fledged in August, or both.

Our information permits us to characterize fairly accurately the tim-

ing of events in the breeding cycle of the Least Flycatcher at a northern latitude. The pre-egg stage in 1981 was about 13 days. This was from the time known residents of the study area had returned in spring (19 May, see Table 1) to 31 May, the date the first eggs were laid in this population (Fig. 2). To the pre-egg stage is added egg laying (3 days, for the usual clutch of 4 to be completed), incubation (13 days), nestling period (15 days), and post-fledging parental care (at least 14 days) for a nesting cycle and period spent on the breeding grounds of about 58 days. This figure is remarkably close to Hussell's (1981) calculation of 64 days, based on 3 years' of migration data at Long Point, Ontario. In fact, our figure may be slightly conservative, therefore making it almost identical to Hussell's.

Hussell (1981) commented on the remarkably short time adult Least Flycatchers, at least those successful in their initial breeding attempts, spend on the breeding grounds. The adults' early departure for the wintering areas in Central America has been considered to be related to the post-migratory timing of the molt of the flight feathers (Dwight 1900, Johnson 1963, Hussell 1980). Most passerines molt on the breeding grounds before migrating in the fall. The timing of the wing molt of the Least Flycatcher is therefore unusual for passerines and migratory birds in general, but occurs also in some caprimulgids (Rohwer 1971), swallows (Dwight 1900), and several other species of tyrannid flycatchers (Johnson 1963, Morehouse and Brewer 1968). The common denominator among these groups that delay their molt is their aerial insect foraging habit, a correlation noted by Johnson (1963). Morehouse and Brewer (1968:54) suggested that "the energetic demands of caring for young over an extended period of time combined with the need to migrate southward before food and weather conditions become unfavorable do not allow an aerial forager sufficient interval for molting." Morehouse and Brewer considered specifically the Eastern Kingbird (*Tyrannus tyrannus*), which exhibits extended post-fledging parental care, often up to their departure (from our study area) in late August. The Least Flycatcher is different. Its 2-week period of post-fledging parental care is not unusually long and although its prey are obtained through aerial maneuvering (mainly hovering), the prey are generally gleaned from foliage (Sherry 1979, pers. obs.). The Orchard Oriole (*Icterus spurius*), a recent colonizer of our study area (Sealy 1980), is also an exception in that it has an extended period of post-fledging parental care and a post-migratory molt but is a substrate gleaner during the breeding season (Sealy 1979).

Rappole and Warner (1980) hypothesized a tropical origin for most nearctic passerine migrants, and their data support Mengel (1964) who favored this view for wood warblers. Fitzpatrick (1980:71) noted that "For well over half the year, eight of the nine migrant *Empidonax* . . . . reside in Central America, where they join five endemic residents in the genus and three other close relatives, currently placed in adjacent genera. With such an array of migrants and residents, similar in both size

and in foraging habits, differences in distribution and habitat use must be paramount in any ecological segregation between them." Fitzpatrick (1980) showed that several wintering *Empidonax* species exhibit such distributional separation, and Rappole and Warner (1980) showed that Least Flycatchers are territorial. Early departure of adult Least Flycatchers from the breeding ground before the collapse of the food supply, therefore, may be due to competition for winter territories, as Morton (1976) argued for the Yellow Warbler (*Dendroica petechia*). Adult Least Flycatchers may be able to establish and maintain territories in Central America, but it is unlikely that juveniles are able to do so. Age-related differences in the ability to hold territories on the wintering grounds have been found in Yellow Warblers (Morton 1976) and Dark-eyed Juncos (*Junco hyemalis*) (Ketterson and Nolan 1979) and probably are common in many passerine species. Thus, there is probably no advantage to juvenile Least Flycatchers to migrate early.

ACKNOWLEDGMENTS

This study was funded by a grant (A9556) from the Natural Sciences and Engineering Research Council of Canada to S. G. Sealy. We thank R. M. R. Barclay, H. E. den Haan, and D. M. Guinan for assistance with various aspects of the fieldwork. D. J. T. Hussell critically read drafts of the manuscript and offered several useful suggestions for its improvement. The continued support of J. M. Shay, Director, and staff and students at the University of Manitoba Field Station (Delta Marsh) is greatly appreciated. We are grateful to the Portage Country Club for granting us permission to conduct some of this work on their adjacent property. This paper is contribution number 87 of the University of Manitoba Field Station (Delta Marsh).

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